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Post-fire tree establishment patterns at the alpine treeline ecotone: Mount Rainier National Park, Washington, USA

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Abstract

Questions: Does tree establishment: (1) occur at a treeline depressed by fire, (2) cause the forest line to ascend upslope, and/or (3) alter landscape heterogeneity? (4) What abiotic and biotic local site conditions are most important in structuring establishment patterns? (5) Does the abiotic setting become more important with increasing upslope distance from the forest line?

Location: Western slopes of Mount Rainier, USA.

Methods: We performed classification analysis of 1970 satellite imagery and 2003 aerial photography to delineate establishment. Local site conditions were calculated from a LIDAR-based DEM, ancillary climate data, and 1970 tree locations in a GIS. We used logistic regression on a spatially weighted landscape matrix to rank variables.

Results: Considerable establishment after 1970 caused forest line elevation to increase over 150 m in specific locations. Landscape heterogeneity increased with distance from the 1970 forest line. At a broad spatial context, we found establishment was most common near existing trees (0-50 m) and at low elevations (1250-1350 m). Slope aspect (W, NW, N, NE, and E), slope angle (40-60°), and other abiotic factors emerged as important predictors of establishment with increasing upslope distance from the forest line to restricted spatial extents.

Conclusions: Favorable climatic conditions likely triggered widespread tree establishment. Readily available seed probably enhanced establishment rates near sexually mature trees, particularly in the less stressful environment at low elevations. The mass effect of nearly ubiquitous establishment in these areas may have obscured the importance of the abiotic setting to restricted spatial extents. Topographic variability apparently produced favorable sites that facilitated opportunistic establishment with increasing upslope distance from the forest line, thereby enabling additional trees to invade the alpine tundra.

Keywords: *Abies lasiocarpa*; CORONA; Hierarchical partitioning; Landscape; Pacific Northwest; Seed dispersal; Spatial autocorrelation; Subalpine parkland; Topography.

Abbreviations: DEM = digital elevation model; DOQQ = digital orthophoto quarter quadrangle; GIS = geographic information system; LIDAR = light detection and ranging.

Nomenclature: Anon. (1993).

Introduction

The alpine treeline ecotone (treeline) exhibits one of the most striking transitional physiognomic landscapes, which has garnered attention from vegetation scientists interested in assessing the floristic impacts of climate change (Walther 2003). Treelines often display remarkable variability in structure and composition between different regions, thus contributing to a wide range of definitions (Holtmeier 2003). Simply stated, the treeline demarcates the boundary between closed forests at low elevations and the alpine tundra at high elevations. In the Pacific Northwest, this boundary is characterized by a broad ecotone extending from closed canopy forest through subalpine parklands, to the scrub line or upper limit of trees (Franklin & Dyrness 1988). The subalpine parkland is comprised of a mosaic of tree clusters and herbaceous vegetation, often extending over an elevation gradient of 300-400 m. The upper limit of this zone is variable and may be composed of krummholz (German for short crooked trees) or upright arboreal vegetation.

The traditional paradigm contends that temperature controls altitudinal limits of treelines and that observed upslope advance is the most likely response to climatic warming (cf. Daniels & Veblen 2003). However, others caution that disturbances

(Daniels & Veblen 2003; Cairns & Moen 2004) and variability of tree responses to local site conditions (Miller & Halpern 1998; Holtmeier & Broll 2005) may confound interpretations, making any direct connections to climate tenuous. Reports of relatively stable treelines over the last 50 years warrant these concerns (e.g. Cuevas 2002; Klasner & Fagre 2002). The paucity of known relationships between disturbance events, climate, local site conditions, and altitudinal limits of treelines necessitates additional research to place observed treeline positions in a climatic context (Daniels & Veblen 2003; Holtmeier & Broll 2005).

Many treeline studies are intentionally executed at relatively undisturbed sites in an attempt to correlate results with climatic fluctuations and thus avoid what is perceived to be confounding influences from disturbances (e.g. Cuevas 2002). We assert that disturbed treelines are equally useful to study, given that upslope advance of treelines is often impeded by local site conditions, despite favorable climatic influences, and that some treelines are relicts of past climates (Holtmeier 2003; Lingua et al. 2008). Local site conditions that structure establishment patterns (i.e. spatial arrangement of newly established trees) at disturbed treelines may resemble those at relatively undisturbed sites. Thus, studying both can contribute to a better understanding of factors controlling treeline.

Fire is an important disturbance agent capable of destroying existing trees and depressing the altitudinal limits of treelines (Wilson & Agnew 1992; Noble 1993). Many studies have utilized field plots and dendroecology at local scales to assess treeline recovery after a fire event. Bollinger (1973), for instance, analyzed tree rings from the Colorado Front Range and concluded that fire suppresses treelines to new climatically controlled positions where recently established herbaceous cover inhibits treeline recovery. In the same study area, Peet (1981) argued that fire and climate cause treelines to exist in dynamic equilibrium, whereby treelines recover slowly after a fire event, with the highest rates of establishment occurring uniformly near existing trees. He predicted future fires would prevent treelines from reaching altitudinal limits controlled by climate. Shankman (1984) demonstrated that the Colorado Front Range treelines slowly established upslope after a fire disturbance, with the greatest recovery rates occurring at low elevations and in close proximity to existing trees. He posited that treelines could recover to their original altitudinal limits gradually and in a uniform manner, provided that there are no additional disturbances.

Additional studies have illustrated the importance of local site conditions. Agee & Smith (1984) determined that close proximity to patches of surviving trees and lack of deep snow cover were directly related to the highest rates of establishment after fire in the Olympic Mountains, Washington. In the Colorado Front Range, Shankman & Daly (1988) determined that topographically sheltered sites exhibited high rates of establishment after fire and predicted that the treeline would return to its pre-disturbed altitudinal position in a patchy manner. They also noted that a few topographically exposed sites having xerophytic tree species experienced increased rates of establishment. Noble (1993) developed raster-based models depicting interactions between fire disturbance, climate, and subsequent establishment at the treeline. He proposed that upslope treeline advance after fire would be episodic and exhibit heterogeneous establishment patterns.

Clarifying the importance of local site conditions in structuring establishment patterns at the treeline requires the use of a complex landscape ecological approach (Holtmeier 2003). We used satellite imagery, aerial photography, digital terrain data, and ancillary climate data in a GIS environment to explain landscape-scale patterns of establishment at a treeline disturbed by a 1930 fire in Mount Rainier National Park. We suspect that establishment and upslope advance of the forest line will be evident because climate has been generally favorable (i.e. warm and dry summers) throughout the 20th century, particularly on the western slopes of Mount Rainier (Rochefort & Peterson 1996; Miller & Halpern 1998). Landscape heterogeneity will probably decrease near the forest line because of increased seed availability and less stressful environmental conditions. Whereas, we expect heterogeneity will increase beyond the forest line because of distance- and elevation-induced seed dispersal decay combined with a tendency for opportunistic establishment in an increasingly unfavorable environment. We also expect favorable locales to exist throughout the abiotic setting (e.g. slope aspect, slope angle, moisture potential, snow potential, and erosion potential), and these will be important in structuring establishment patterns with increasing upslope distance from the forest line.

Materials and Methods

Study area

Mount Rainier (4392 m) is a well-known volcano and the sister mountain to Mount Fuji in Japan.

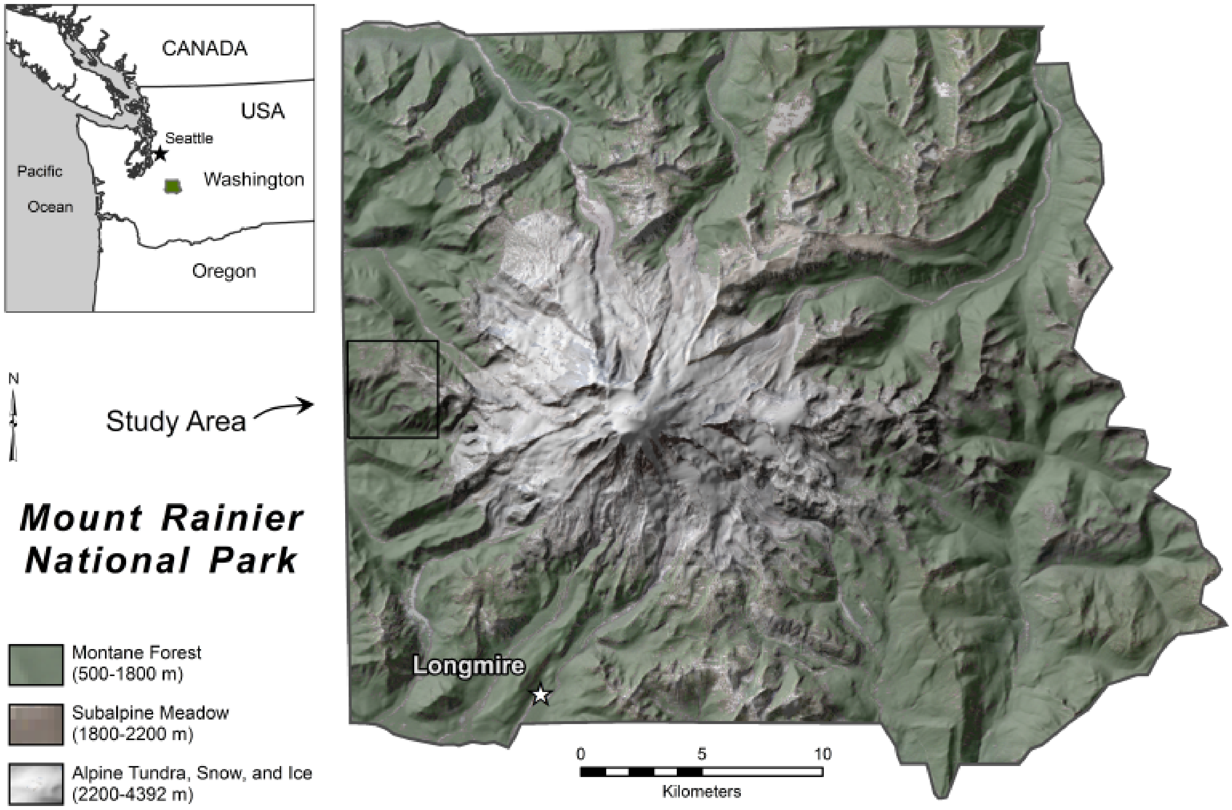

Fig. 1. The study area as denoted by modified September 2000 Landsat ETM+ imagery and a shaded 10-m DEM.

The volcano is nearly symmetrical and is located in the Cascade Range in Washington State, USA (Fig. 1). Deep valleys and many steep ridges consisting of andesite scoured by Pleistocene and early Holocene glaciers dominate the landscape. Along with glacial drift (Crandell 1969), this has created complex topographic features with widely varying microclimates that often influence patterns of treelines (Rochefort & Peterson 1996). Climate in the region can be characterized as humid temperate, with the majority of seasonal precipitation falling as snow or rain during cool winters (Bailey 1995). Prevailing southwesterly winds create a pronounced orographic effect, resulting in heavy annual snowfall of 1000-2000 cm year^{-1} on the western slopes of Mount Rainier (Hemstrom & Franklin 1982; Bailey 1995). Data from the Longmire weather station (elevation 842 m; Fig. 1) (1978-2006) indicate average monthly temperature ranged from -0.3°C in December to 16.0°C in August, average annual precipitation (rain and melted snow) was 201.4 cm, and average annual snowfall was 344.2 cm.

Snowpack may persist well into August on the western slopes, thus shortening the growing season and contributing to relatively depressed treeline elevations (~1500 m) compared to the eastern slopes (~2200 m) and other western USA treelines (Taylor 1922). The patchy structure of the subalpine parkland is thought to be primarily maintained by the depth and duration of snowpack (Henderson 1974; Franklin & Dyrness 1988). Treeline conifers include *Abies lasiocarpa*, *Chamaecyparis nootkatensis*, and *Tsuga mertensiana* that predominate on the mesic western slopes of Mount Rainier. *Pinus albicaulis* and *Picea engelmannii* are most common on the xeric eastern slopes (Rochefort & Peterson 1996). Pulses of increased establishment have been documented throughout the western half of the park during periods of warm dry summers (Franklin et al. 1971; Rochefort & Peterson 1996).

Fire is the predominant disturbance agent in the park, having affected over 90% of existing tree stands, including some treelines (Hemstrom & Franklin 1982). A 1930 fire severely burned extensive areas of high-elevation forest and subalpine parkland (1500-1800 m) near the North Puyallup River, effectively lowering the existing treeline (Hemstrom & Franklin 1982). The aerial extent of the study area is defined by the northeast Mount Wow DOQQ, which was broadly impacted by the

1930 fire. The delineated area contains approximately 150 ha of burned treeline and captures part of the steep southwest-northeast elevation gradient from the North Puyallup River (~800 m) to overarching ridges (~2000 m). The relatively xeric south and west slopes of the steepest ridges were severely burned to the krummholz (Hemstrom & Franklin 1982). Field surveillance in 2006 did not reveal any notable signs of other disturbances, such as avalanches, insect infestations, or disease.

The burned area includes numerous spurs that dissect broad south- and west-facing slopes containing complex microtopography, which can influence tree establishment patterns. *Abies lasiocarpa* is the most prevalent species near the forest line and at the upper limits of the krummholz. This species is a common invader after subalpine parkland fires, with a preference for mildly xeric sites that are topographically protected (Shearer 1984; Miller & Halpern 1998). Wind-driven seed dispersal may carry seeds up to 80 m beyond sexually mature trees ($\geq$ 20 years old) (Noble & Ronco 1978). *Pinus albicaulis*, *Tsuga mertensiana*, and *Chamaecyparis nootkatensis* are also present, but are much less abundant.

Image preprocessing

The United States Geological Survey provided KH-4B satellite imagery from the CORONA mission 1110 for 02.06.1970. The imagery was from the aft camera and scanned at 7 μm, with a spatial resolution of ~1.9 m (McDonald 1995). We orthorectified this imagery using a parametric model and nearest neighbor resampling (Jensen 2005), in concert with direct linear transformation and bundle adjustment to build the exterior orientation (Fiore 2001). A 1.0-m United States Geological Survey color DOQQ from 21.07.2003 was used as the base aerial photography to collect ground control points (Davis & Wang 2003). We selected 42 control points that were evenly distributed throughout the 1970 imagery, with a root mean-square error of 0.495 (Jensen 2005). We used a LIDAR-based 1.8-m DEM (Terrapoint 2003) and KH-4B satellite specifications from declassified documents (McDonald 1995) to model the terrain and satellite position during orthorectification. Pre-processing procedures were employed to remove systematic errors from the DEM (Keqi et al. 2003; Rottensteiner et al. 2005) and the Minnaert correction was used to mitigate radiometric variability from the imagery, which is common in mountainous areas (Itten & Meyer 1993).

We implemented similar methods to georeference aerial photography from 1955, but we could not model the position of the airplane because of insufficient metadata. Also, clouds obscured some key areas of establishment in the photography and some locales also appeared to be pixilated. Thus, the photography was not deemed suitable for detailed mapping procedures or inclusion in the landscape metrics and statistical analyses. However, the photography did allow a qualitative assessment of tree locations before 1970.

Imagery classification, treeline identification, and change detection

We used supervised classifications tailored for high-spatial resolution panchromatic imagery to delineate trees in 1970 and 2003 (Bai et al. 2005). The green band of the DOQQ was separated for the classification analysis because the signal closely corresponds to the KH-4B panchromatic band. The green band of the DOQQ was resampled with the nearest neighbor method to match the ~1.9-m spatial resolution of the KH-4B imagery (Jensen 2005). Next, we selected 10 000 training points for each classification category representing trees, shadows (from trees), and treeless areas. We implemented a minimum distance supervised classification with a fitted modal filter to assign shadows to either trees or treeless areas, resulting in a binary classification of trees versus treeless areas.

Upper elevations (~1500 m and above) in the KH-4B imagery displayed areas of residual snowpack near some tree patches. We used 1969 aerial photography that lacked snowpack to verify whether any trees were obscured by snow, and the classification was adjusted accordingly.

The forest line was used to determine the lower boundary of the treeline and as an easily identifiable reference point for assessing treeline changes in terms of distance and elevation (Jobbagy & Jackson 2000). We visually identified and digitized the approximate position of the forest line in the 1955 imagery. Forest line in the classified 1970 satellite imagery and 2003 aerial photography was identified by using a GIS to detect the highest altitudinal limits of pixels classified as trees that were contiguously connected to closed forest. We quantified maximum and minimum forest line changes in a GIS by assessing upslope measurements from each pixel in the 1970 forest line that were perpendicular to slope contours. Treeline was defined as all pixels 30 m below the 1970 forest line and continuing to the highest elevations attained by pixels classified as trees in the 2003 aerial photography for inclusion in the landscape metrics and statistical analyses. Last, change detection was performed to identify areas of establishment at the treeline between 1970 and 2003.

Landscape metrics

The spatial complexity and variability of patch mosaics, otherwise known as landscape heterogeneity, often signify the presence of multiple underlying ecological processes (Li & Reynolds 1994). Studying the spatial arrangement of patches in relation to other abiotic and biotic variables can provide valuable insight to potentially causative ecological mechanisms involved in structuring patch mosaics (Li & Reynolds 1994). To characterize the influence of establishment on landscape heterogeneity, we used a robust landscape metric (new contagion index) and establishment rates in six different zones throughout the treeline (Li & Reynolds 1993). Elevated establishment rates combined with a more fragmented or heterogeneous landscape (i.e. low contagion value) in a particular zone indicate unique combinations of specific local site conditions that may be producing an environment more favorable for establishment.

The first zone created (A) began 30 m downslope from the 1970 forest line and proceeded 100 m upslope, closely following the curvature of the forest line. The remainder (B, C, D, E, and F) was comprised of five separate 100-m zones proceeding sequentially beyond zone A across the subalpine parkland and towards the alpine tundra. We selected 100-m zones because establishment rates beyond the 1970 forest line were sigmoidal, and each zone spanned a particular section of the sigmoidal curve. A new contagion index was calculated for each zone in the 1970 satellite imagery and 2003 aerial photography. Contagion values from 1970 were subtracted from values in 2003. Negative and positive results indicate increased and decreased landscape heterogeneity, respectively. We also determined establishment rates in each zone by dividing the number of pixels classified as trees in 2003 by the number of pixels classified as treeless in the 1970, then multiplying by 100.

Ground verification and accuracy assessment

We marked 60 ground verification points with a WAAS corrected global positioning system and used them to confirm mapped areas of establishment in the 1970 satellite imagery and 2003 aerial photography. Due to poor satellite reception, we marked 23 additional points with an uncorrected global positioning system in patches of old-growth trees. In the field, we visually identified 49 relatively stable points (i.e. 26 barren patches of rocks that did not exhibit recent signs of disturbance or vegetative growth nearby, and 23 patches of large old-growth trees). To verify the ages of young trees mapped on the imagery (i.e. 33 years or less), 15 tree ring cores and 19 cross sections were collected from widely distributed areas (Jensen 2005) within or in close proximity to mapped patches of establishment. We subjected the tree samples to standard processing before counting tree rings and determining tree ages (Fritts & Swetnam 1989). The resulting classification accuracy was 89.2% for the 1970 points and 91.6% for the 2003 points.

Local site conditions

Data for a suite of variables thought to influence establishment patterns were obtained from the processed DEM and ancillary climate data. Elevation values were extracted directly from the DEM. We calculated slope aspect and slope angle with a 3×3 window while considering all eight surrounding pixels (Burrough & McDonnell 1998). We calculated snow index values from curvature (Zevenbergen & Thorne 1987; Moore et al. 1991), southwesterly prevailing winds, elevation, slope aspect, and slope angle (Frank 1988; Burke et al. 1989; Brown 1994). Topographic concavities and leeward slope aspects at high elevations were weighted with the highest snow potential (i.e. likely to have deep season-shortening snowpack). We calculated wetness index values from the upslope catchment area and drainage patterns quantified in the DEM (Beven & Kirkby 1979; Brown 1994). Enclosed depressions with large upslope moisture catchment areas were weighted with the highest wetness potential (i.e. likely to have moist and cool soils). We determined sediment erosive index values by considering calculations of slope angle and flow accumulation from the DEM (Moore et al. 1993). Steep convex landscape features and open concavities with large upslope moisture catchment areas (e.g. ravines and stream beds) were weighted with the highest erosion potential (i.e. surfaces likely to be regularly disturbed by erosive forces). Proximity to and direction from trees existing in 1970 was calculated with standard Euclidean distance measures using the 1970 trees as source areas.

Statistical analyses

We devised a statistical approach to test the general null hypothesis that establishment patterns were not related to local site conditions. We selected binomial logistic regression for the statistical analyses because the data consisted of a nominal dependent variable with two classes and independent variables with continuous data. To assess the potential of inflated R^2 values associated with multicollinearity, we conducted Pearson correlation tests between the independent variables of 1000 randomly sampled points (Mac Nally 2000). No pairs were found to be greater than the 0.7 threshold recommended by Hosmer & Lemeshow (2000). However, we found that elevation had values above 0.6 when considered with proximity to 1970 trees and slope angle. To mitigate the effects of multicollinearity, we used *R 2.4.1* (Anon. 2006) to conduct binomial logistic regression within the hierarchical partitioning framework (Chevan & Sutherland 1991; Mac Nally 1996) and determined the relative amount of variance each independent variable contributed to establishment patterns (Mac Nally 2002). All circular independent variables (i.e. slope aspect and direction from 1970 trees) were sine-transformed to a linear format ranging from -1 (south) to 1 (north) (Zar 1999). The dependent variable was assigned 0 (treeless) and 1 (trees). Independent variables exhibited significant skewness (1.3–1.9) and kurtosis (1.1–1.7). We excluded outliers and modified the data via logarithmic and square root transformations to reduce skewness and kurtosis values below 0.5. We used a modified randomization approach with *R 2.4.1* (2006) to obtain *Z*-values and determine whether the contribution of each independent variable was statistically significant (Mac Nally 2002). Overall, the variance explained by each independent variable with this regression technique can be substantially lower than results acquired from traditional approaches (e.g. stepwise regression) because joint contributions from correlated independent variables and inflated R^2 values are mitigated (Mac Nally 2000).

Failure to account for spatial autocorrelation can confound statistical analyses of ecological phenomena and may result in the erroneous identification of important independent variables and their relative rankings (Griffith & Peres-Neto 2006). To address spatial autocorrelation, we used *R 2.4.1* (2006) to implement a modification of the principal coordinates of neighbour matrices approach based on eigenvectors and distance (Dray et al. 2006). We selected the Delaunay triangulation to generate the spatial weights matrix based on data-driven Akaike information criterion rankings. Results consisted of positive (i.e. similar neighbors clustered in space) and negative (i.e. dissimilar neighbors) eigenvalues in continuous data formats that corresponded well with the traditional Moran's I measure of spatial autocorrelation. We included these data as an additional independent variable in the regression analyses (Griffith & Peres-Neto 2006).

We repeated the method for each zone (A-F) discussed with the landscape metrics to gauge whether the abiotic setting becomes more important in structuring establishment patterns with increased upslope distance from the forest line. Two hundred and fifty points were randomly sampled from each zone and subjected to additional tests. After a preliminary analysis, we combined the two zones closest to the forest line (A and B) and the two zones furthest away from the forest line (E and F) because they gave similar results.

Results

Forest line changes, landscape heterogeneity, and establishment rates

The 1970 forest line was clearly higher than the approximated elevation of the 1955 forest line, but quantifying establishment rates between these dates was not possible due to the qualitative methods involved in assessing the 1955 imagery (Fig. 2). The average elevation of the forest line in the 1970 imagery was approximately 1343 m, with a minimum of 1280 m and a maximum of 1475 m (Fig. 2). The forest line had ascended upslope by 2003 to an average elevation of approximately 1453 m, with a minimum of 1400 m and a maximum of 1527 m. The smallest altitudinal forest line change between 1970 and 2003 was 0.0 m and the largest was 152 m. The smallest distance of forest line change was also 0.0 m and the largest was 264 m. We observed the majority of establishment near the lowest forest line elevation of 1280 m in the 1970 imagery and the least near the uppermost forest line elevation of 1475 m in the 1970 imagery, with the notable exception of a bare patch between 1300 and 1400 m.

We conducted the following analyses in six zones placed throughout the previously defined treeline area. Contagion difference values were 39% for zone A (Fig. 3); these decreased in zones B (-36%), C (-45%), and D (-63%) before rebounding slightly in zones E (-62%) and F (-42%) (Fig. 3). The highest establishment rates occurred in zone A (88%) and steadily decreased in zones B (69%), C (49%), D (42%), E (27%). and F (12%) (Fig. 4).

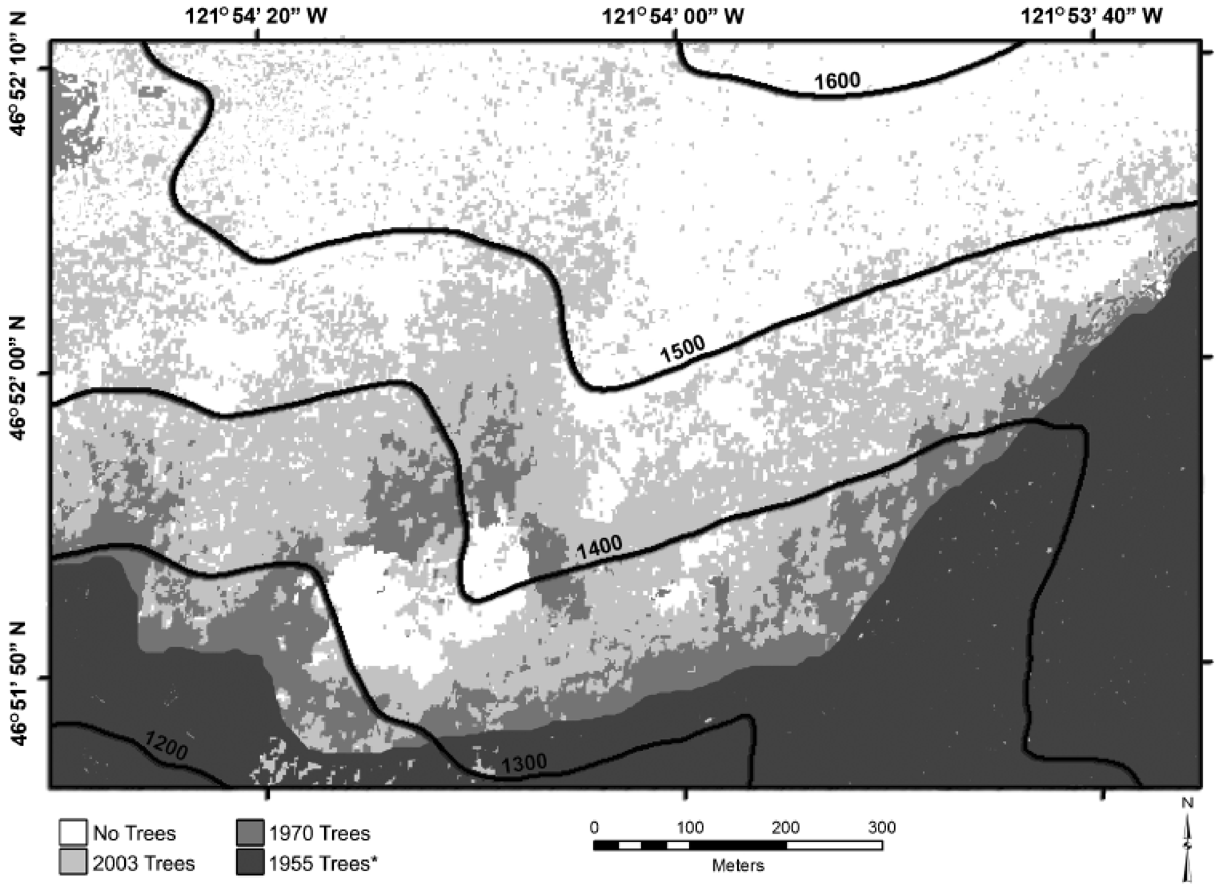

Fig. 2. Landscape patterns of tree establishment at the study site based off digitized 1955 aerial photography and classification analysis of 1970 CORONA satellite imagery and 2003 aerial photography. Dark gray denotes the approximate location of the forest line and contiguously connected trees in 1955. Medium gray represents trees present in 1970. Light gray represents trees that were newly established after 1970 and prior to 2003. The 1970 forest line follows the northern fringe of continuously connected forest depicted by the medium gray pixels. The 2003 forest line follows the northern fringe of continuously connected forest depicted by the light gray pixels. * indicates an approximation based on observations in a GIS.

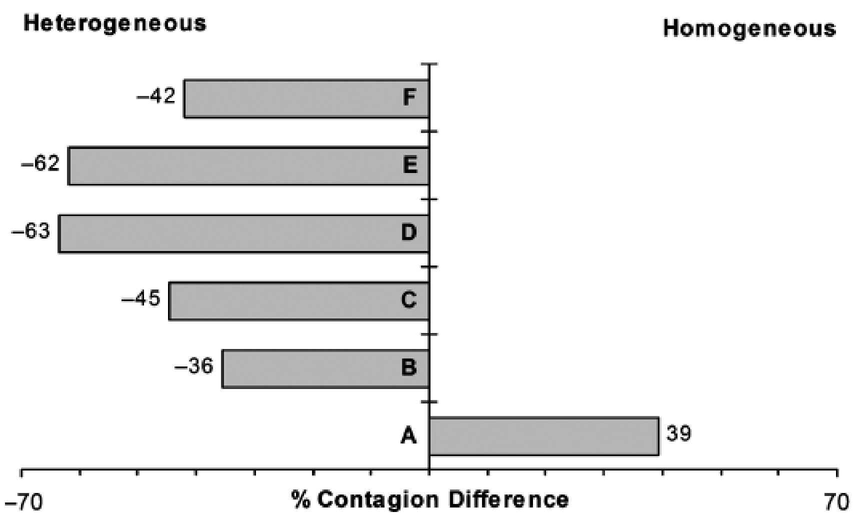

Fig. 3. Contagion differences measuring landscape heterogeneity changes between 1970 and 2003 for six consecutive 100-m zones. Zone A begins 30 m below the 1970 forest line and zone F is at the altitudinal limit of 2003 trees. Each zone follows the curvature of the forest line.

Local site conditions influencing patterns of establishment

We rejected the general null hypothesis and accepted the alternative hypothesis that local site conditions were related to establishment patterns. At a broad spatial scale (i.e. entire study area), we discovered that proximity to 1970 trees (14.1%) and elevation (11.6%) were the two most important local site conditions influencing landscape patterns of establishment (Fig. 5). Locales within 50 m of 1970 trees experienced the highest rates of establishment (~75%), before tapering off at a distance of 300 m (< 10%) (Fig. 6a). Locales between 1250 and 1350 m experienced the highest rates of establishment (~80%), before gradually decreasing near 1650 m (~0%) (Fig. 6b). The elevation response also showed a definitive sigmoidal wave pattern.

Slope angle (1.9%) and slope aspect (1.4%) were also influential in structuring landscape patterns of tree establishment (Fig. 5). Moderately steep slope angles between 40° and 60° experienced the highest rates of establishment (~75%). Establishment was less likely on slope angles < 40° and > 60° (< 60%) (Fig. 6c). In terms of slope aspect, west-, northwest-, north-, northeast-, and east-facing slopes displayed elevated rates of establishment (> 80%). Relatively exposed south-facing slope aspects experienced lower establishment rates (~40%) (Fig. 6d).

Direction from 1970 trees (0.6%), wetness index (0.6%), snow index 0.4%), and erosion index (0.3%) were also statistically significant variables that influenced tree establishment patterns (Fig. 5). Leeward and relatively shaded northwest-, north-, and northeast-facing tree patch edges showed the highest rates of establishment. Decreased rates of establishment occurred on south-facing tree patch edges. Xeric to slightly mesic locales experienced the highest rates of establishment. However, extremely wet locales experienced lower establishment rates. Locales with moderate snow potential displayed elevated rates of establishment, before tapering off near exposed windblown areas and in protected sites

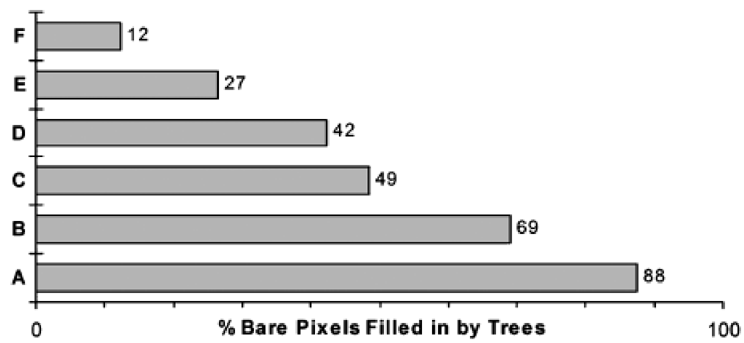

Fig. 4. Percentage of bare 1970 pixels filled by trees prior to 2003 for six consecutive 100-m zones. Zone A begins 30 m below the 1970 forest line and zone F is at the altitudinal limit of 2003 trees. Each zone follows the curvature of the forest line.

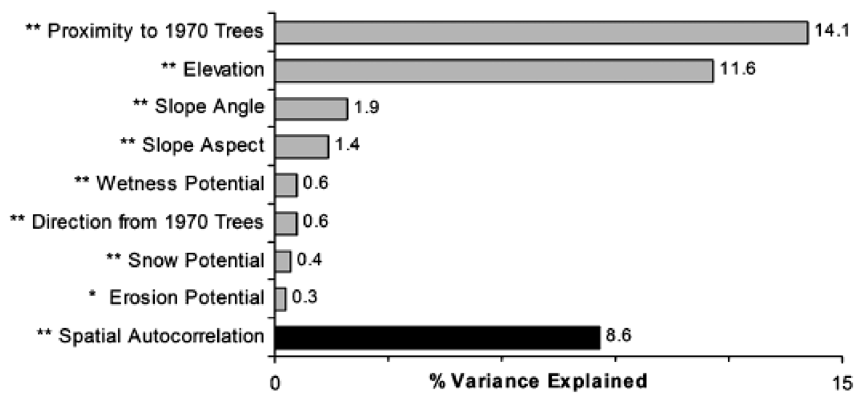

Fig. 5. Percentage of post-1970 tree establishment variance explained by local site conditions within a defined treeline area from 30 m below the 1970 forest line to the altitudinal limit of 2003 trees. Results are based on binomial logistic regressions employed in the hierarchical partitioning framework when considering the entire study area. ** indicates the independent variable is significant at the 99% confidence level, and * indicates significance at 95%.

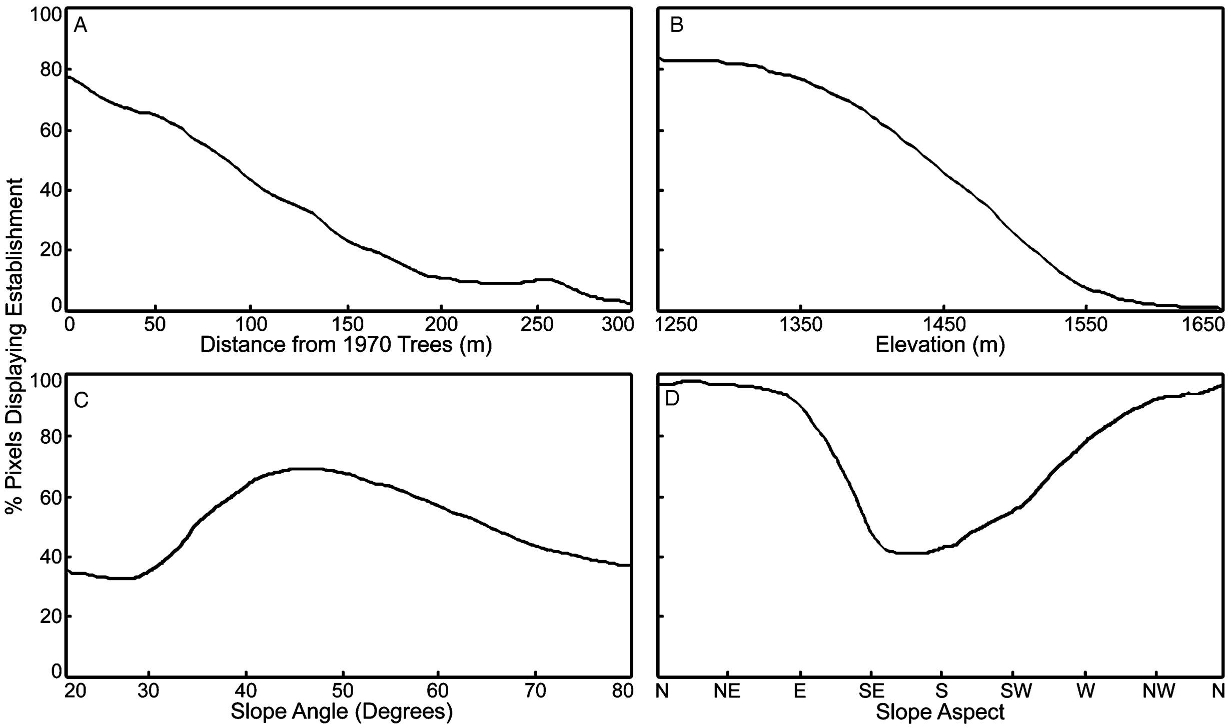

Fig. 6. Relationships between the four most significant local site conditions and post-1970 tree establishment patterns based on a defined treeline area from 30 m below the 1970 forest line to the altitudinal limit of trees in the 2003 imagery. Values were calculated from 10 000 points used in a stratified sampling scheme in order to reduce spatial autocorrelation. Fractions of pixels experiencing tree establishment were calculated at 50-pixel intervals for each independent variable (i.e. number of pixels classified as trees in the 2003 imagery divided by 50), converted to a percentage, plotted, and connected in a smoothed line graph.

with high snow potential. Locales prone to erosion displayed slightly decreased establishment rates compared to protected locales. Individually, none of these local site conditions explained $>2\%$ of the potential variance at a broad spatial scale. However, they became more important, along with slope aspect and slope angle, when examined at restricted spatial scales.

When considering the local site conditions in each of the six zones, we observed elevated establishment rates at locales similar to those reported in the three preceding paragraphs. However, there were palpable differences in the statistically ranked order of local site conditions. The two zones nearest the 1970 forest line (A and B) became nearly fully occupied by new trees and thus exhibited suppressed signals. However, we observed results in zone C nearly matching those of the entire study area, except for a peak in the importance of slope aspect (Figs 5 and 7). Several abiotic factors emerged as very important predictors of establishment with increased upslope distance from the previous zone. Slope aspect (13.1%) was the most important variable in zone D. Slope angle (5.7%) and other abiotic variables also became more important; however, proximity to 1970 trees (11.3%) and elevation (5.8%) remained important predictors in zone D. In zones E and F, the cumulative explanatory power of the local site conditions decreased slightly, with slope aspect (8.5%) and proximity (6.5%) to 1970 trees being the most important.

Discussion

Broad establishment trends

Favorable climatic conditions (i.e. warm and dry summers) probably triggered widespread establishment between 1955 and 2003. Initially, the abiotic setting appeared to play only a minor role in structuring establishment patterns. The majority of establishment occurred near existing trees and at low elevations, regardless of topographic variability; accounting for decreased landscape heterogeneity in zone A and upslope advancement of the forest line. Previous researchers have documented similar es-

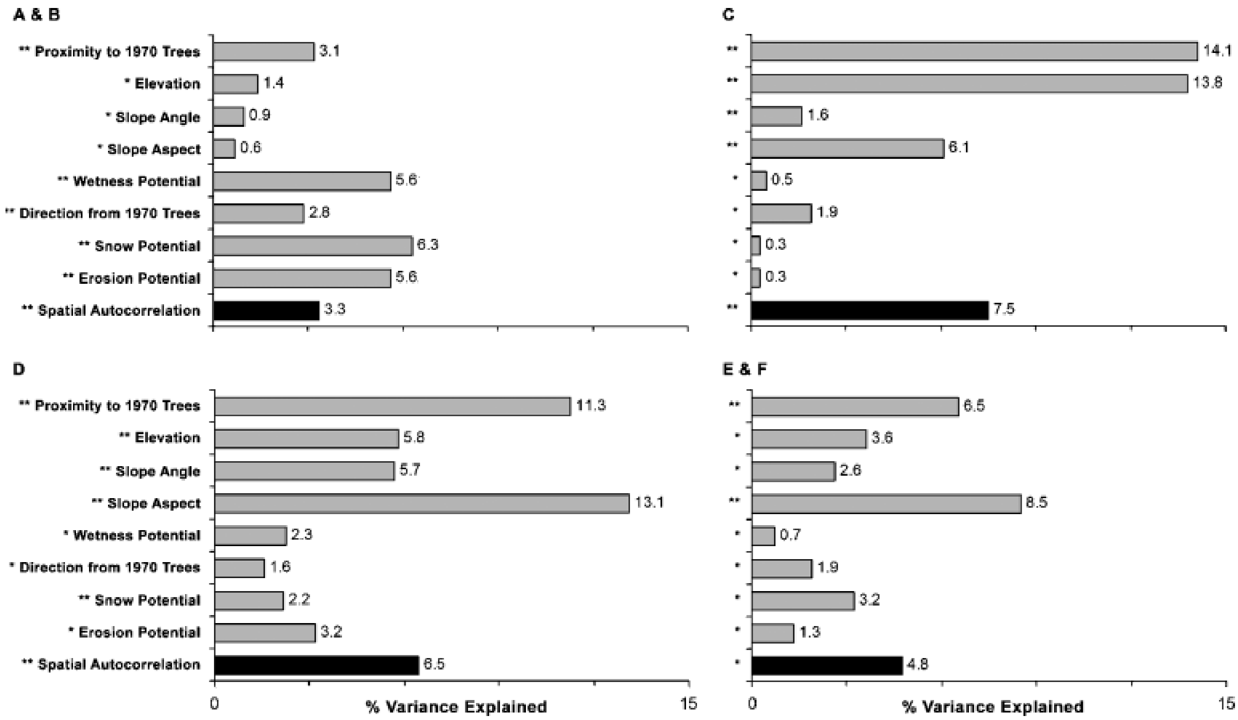

Fig. 7. Percentage of post-1970 tree establishment variance explained by local site conditions in six zones within a defined treeline area from 30 m below the 1970 forest line to the altitudinal limit of 2003 trees. Distances upslope from the 1970 forest line include 0-200 m (zones A and B), 200-300 m (zone C), 300-400 m (zone D), and 400-600 m (zones E and F). Results are based on binomial logistic regressions employed in the hierarchical partitioning framework. ** indicates the independent variable is significant at the 99% confidence level, and * indicates significance at 95%.

tablishment patterns after fire disturbance (e.g. Peet 1981; Agee & Smith 1984; Shankman 1984).

We attribute high establishment rates at these locales mostly to increased seed availability from nearby and upslope trees, but also partly to less stressful environmental conditions at low elevations (Agee & Smith 1984; Shankman & Daly 1988; Holtmeier 2003). It is difficult, however, to ignore the possibility that positive feedback mechanisms may be enhancing establishment rates at this site. Contemporary research conducted on positive feedback at the alpine tundra ecotone (e.g. Alftine & Malanson 2004; Bekker 2005; Resler 2006) suggests that it may play a critical role in structuring observed establishment patterns. Mature trees ameliorate the microclimate by increasing soil moisture-holding capacity, moderating soil temperatures, improving nutrient conditions, lengthening the growing season, and protecting seedlings from wind (Little et al. 1994; Weisberg & Baker 1995); thus initiating landscape-scale positive feedback changes into nearby exposed areas (Resler et al. 2005; Cerney 2006; Resler 2006). These assertions are consistent with the literature, which suggests establishment is highest adjacent to clusters of existing trees, before declining with distance in treeline environments (e.g. Peet 1981; Shankman 1984).

Changing roles of abiotic and biotic factors

Landscape heterogeneity was probably enhanced by reduced tree establishment rates with increases in upslope distance from the forest line (zones B-F). Heterogeneous establishment patterns throughout these zones suggest establishment became more opportunistic and that different local site conditions may be more important at restricted spatial scales. Indeed, the abiotic setting appeared to produce favorable establishment sites (e.g. protected slope aspects, moderate slope angles, moderate snow potential, moderate to low wetness potential, and low erosive potential) at high elevations beyond the forest line (zones C-F) that rivaled or became more important than proximity to existing trees and elevation (Fig. 7). These heterogeneous establishment patterns match predictions of patchy and variable establishment after fire disturbance, as dictated by a combination of slope aspect, slope angle, soil moisture, and snowpack (Shankman & Daly 1988; Noble 1993).

Potential establishment at high elevations beyond the forest line may be limited by seed dispersal decay, reduced seed viability, and approaching the physiological threshold for trees (Baig & Tranquillini 1976; Tranquillini 1979). Wind Wizard (Butler et al. 2006) suggests that the topography in the study area has a strong effect on winds, forcing the prevailing southwesterly winds, as well as westerly and northerly winds, mostly upslope, which likely carry high quantities of wind-dispersed seed (e.g. *Abies lasiocarpa)* to distant meadows. The upper threshold of seed dispersal decay is probably most limiting to establishment at the highest elevations. However, the abiotic setting appears to be crucial for facilitating establishment within the upslope seed dispersal zone at exposed locales in the harsh environment at high elevations. The sigmoid pattern of establishment we observed with elevation supports this assertion because it indicates competition between patches of different vegetative functional groups and associated influences from ecological site factors are more pronounced at high elevations, thereby reducing establishment rates (Cairns & Waldron 2003).

High rates of establishment on west-, northwest-, north-, northeast-, and east-facing slope aspects can probably be attributed to the existence of narrow diurnal to nocturnal temperature ranges, which produce fewer tree seedling fatalities when compared to relatively exposed south-facing slope aspects that are often subjected to high and low temperature extremes (Germino et al. 2002). Increased rates of establishment evident on moderate slope angles may be higher because soil is more developed than at steep slope angles and is less susceptible to geomorphic disturbances (Holtmeier 2003). Decreased establishment rates observed on shallow slope angles probably occur because existing herbaceous cover is more likely to competitively exclude invading trees (Wardle 1985; Holtmeier 2003). Animal use may also influence vegetation patch dynamics on shallow slope angles (Vale 1987; Veblen et al. 2000). These findings are consistent with the topographic preferences of *Abies lasiocarpa*.

Conclusions

This disturbed treeline in this site seems to have entered a phase of rapid establishment, triggered primarily by favorable climatic conditions. If the climate remains favorable, we expect increased seed availability to continue driving widespread establishment near the forest line and near the sexually mature trees. Positive feedback may also be a significant contributor, but our analysis offers mostly circumstantial evidence for this assertion. Reduced rates of opportunistic establishment will likely persist in favorable locales throughout the abiotic setting with increased upslope distance from the forest line. These *eco-incursions* will probably facilitate the ability of trees to become established and reproduce in the distant tundra; thereby accelerating tree invasions into exposed locales. The concerted effect of these processes will probably cause the treeline to ascend upslope. However, the width of the ecotone may become narrower in the future due to enhanced establishment rates near the forest line. Severely burned areas with few or no surviving trees near the former upper tree limit, on the other hand, may require several additional decades to recover.

It is clear that several abiotic and biotic processes are operating at different spatial scales in this study area. Vegetation scientists have long recognized that plot-scale studies may be susceptible to spatially aggregated processes, but our results indicate this phenomenon may be particularly pronounced at the treeline. Remote sensing, GIS, and spatial statistics should serve a more important role in determining suitable locations of field plots or transects. For example, vegetation scientists could use these tools to identify sites inhibiting establishment in the abiotic setting (e.g. exposed slope aspects with low snow potential) and corresponding plots could be set up to determine if microsite conditions are facilitating limited quantities of establishment in such areas.

Finally, we recognize that parts of the observed establishment patterns remain unexplained. Other variables, such as geologic substrate, edaphic properties, and independent responses of species, could modify the establishment patterns. Remnants of burned boles may also contribute to unique patterns of establishment (Little et al. 1994). These variables were either not available at a spatial grain fine enough for inclusion in this study or were indistinguishable on the photography. Future research may include (1) the use of specialized remote sensing platforms to quantify the electrical conductivity of soils and provide additional detailed edaphic information at the landscape scale, (2) plot-scale studies investigating the influences of microsites (e.g. burned boles) and species-specific responses on establishment patterns, and (3) plot-scale studies directly testing the potential influence from positive feedback. Important questions remain as to how the rankings of local site conditions tested here differ at other treelines. We suspect that the rankings are susceptible to change, particularly under different climate regimes and at other types of treeline.

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References

Agee, J.K. & Smith, L. 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. *Ecology* 65: 810–819.

Alftine, K.J. & Malanson, J.P. 2004. Directional positive feedback and pattern at an alpine treeline. *Journal of Vegetation Science* 15: 3–12.

Anon. (Flora of North America Editorial Committee, eds) 1993. *Flora of North America: North of Mexico. Vols I–II*, Oxford University Press, New York, NY, US.

Anon. (R Development Core Team) 2006. *R: a language and environment for statistical computing*. R.D.C.T, Vienna, Austria.

Bai, Y., Walsworth, N., Roddan, B., Hill, D.A., Broersma, K. & Thompson, D. 2005. Quantifying tree cover in the forest-grassland ecotone of British Columbia using crown delineation and pattern detection. *Forest Ecology and Managment* 212: 92–100.

Baig, M.N. & Tranquillini, W. 1976. Studies on upper timberline: morphology and anatomy of Norway spruce (*Picea abies*) and stone pine (*Pinus cembra*) needles from various habitat conditions. *Canadian Journal of Botany* 54: 1622–1632.

Bailey, R.G. 1995. *Description of the ecoregions of the United States*. 2nd ed. USDA Forest Service, Washington, DC, USA.

Bekker, M.F. 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic and Alpine Research* 37: 97–107.

Beven, K.J. & Kirkby, M.J. 1979. The hydrological response of headwater and sideslope areas. *Hydrological Society Bulletin* 23: 419–437.

Bollinger, W.H. 1973. *The vegetation patterns after fire at the alpine forest-tundra ecotone in the Colorado Front Range*. Dissertation, University of Colorado at Boulder, USA.

Brown, D.G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *Journal of Vegetation Science* 5: 641–656.

Burke, I.C., Reiners, W.A. & Olson, R.K. 1989. Topographic control of vegetation in a mountain big sagebrush steppe. *Vegetatio* 84: 77–86.

Burrough, P.A. & McDonnell, R. 1998. *Principles of geographical information systems*. Oxford University Press, New York, NY, USA.

Butler, B.W., Finney, M., Bradshaw, L., Forthofer, J., McHugh, C., Stratton, R. & Jimenez, D. 2006. Wind wizard: a new tool for fire management decision support. In: Andrews, P.L. & Butler, B.W. and comps. *Fuels management – how to measure success: conference proceedings*. pp. 787–796. USDA Forest Service Rocky Mountain Research Station, Fort Collins, CO, USA.

Cairns, D.M. & Moen, J. 2004. Herbivory influences tree lines. *Journal of Ecology* 92: 1019–1024.

Cairns, D.M. & Waldron, J.D. 2003. Sigmoid wave transitions at alpine treeline. *Geografiska Annaler Series A* 85: 115–126.

Cerney, D.L. 2006. *Assessment of landscape change in Waterton Lakes National Park, Canada, using multitemporal composites constructed from terrestrial repeat photographs*. Dissertation, Texas State University at San Marcos, TX, US.

Chevan, A. & Sutherland, M. 1991. Hierarchical partitioning. *American Statistician* 45: 90–96.

Crandell, D.R. 1969. Surficial geology of Mount Rainier National Park, Washington. *USGS Bulletin* 1288: 41.

Cuevas, J.G. 2002. Episodic regeneration at the Nothofagus pumilio alpine timberline in Tierra del Fuego, Chile. *Journal of Ecology* 90: 52–60.

Daniels, L.D. & Veblen, T.T. 2003. Regional and local effects of disturbance and climate on altitudinal treelines in northern Patagonia. *Journal of Vegetation Science* 14: 733–742.

Davis, C.H. & Wang, X. 2003. Planimetric accuracy of IKONOS 1m panchromatic orthoimage products and their utility for local government GIS basemap applications. *International Journal of Remote Sensing* 24: 4267–4288.

Dray, S., Legendre, P. & Peres-Neto, P.R. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* 196: 483–493.

Fiore, P.D. 2001. Efficient linear solution of exterior orientation. *IEEE Transactions on Pattern Analysis & Machine Intelligence* 23: 140.

Frank, T.D. 1988. Mapping dominant vegetation communities in the Colorado Rocky Mountain Front Range with Landsat Thematic Mapper and digital terrain data. *Photogrammetric Engineering and Remote Sensing* 54: 1727–1734.

Franklin, J.F. & Dyrness, C.T. 1988. *Natural vegetation of Oregon and Washington*. Oregon State University Press, Corvallis, OR, US.

Franklin, J.F., Moir, W., Douglas, W. & Wiberg, C. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. *Arctic, Antarctic and Alpine Research* 3: 215–224.

Fritts, H.C. & Swetnam, T.W. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Advances in Ecological Research* 19: 111–188.

Germino, M.J., Smith, W.K. & Resor, A.C. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology* 162: 157–168.

Griffith, D.A. & Peres-Neto, P.R. 2006. Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology* 87: 2603–2613.

Hemstrom, M.A. & Franklin, J.F. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. *Quaternary Research* 18: 32–51.

Henderson, J.A. 1974. *Composition, distribution, and succession of subalpine meadows in Mount Rainier National Park*. PhD dissertation, Oregon State University, Corvallis, OR, US.

Holtmeier, F.K. 2003. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Kluwer Academic Publishers, Boston, MA, US.

Holtmeier, F.K. & Broll, G. 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography* 14: 395–410.

Hosmer, D.W. & Lemeshow, S. 2000. *Applied Logistic Regression*. 2nd ed. Wiley, New York, NY, US.

Itten, K.I. & Meyer, P. 1993. Geometric and radiometric correction of TM data of mountainous forested areas. *IEEE Transactions on Geoscience and Remote Sensing* 31: 764–770.

Jensen, J.R. 2005. *Introductory Digital Image Processing: A Remote Sensing Perspective*. 3rd ed. Prentice Hall, Upper Saddle River, NJ, US.

Jobbagy, E.G. & Jackson, R.B. 2000. Global controls of forest line elevation in the northern and southern hemispheres. *Global Ecology and Biogeography* 9: 253–268.

Keqi, Z., Shu-ching, C., Whitman, D., Mei-Ling, S., Jianhua, Y. & Chengcui, Z. 2003. A progressive morphological filter for removing nonground measurements from airborne LIDAR data. *IEEE Transactions on Geoscience & Remote Sensing* 41: 872.

Klasner, F.L. & Fagre, D.B. 2002. A half century of change in alpine treeline patterns at Glacier National Park, Montana, USA. *Arctic, Antarctic and Alpine Research* 34: 49–56.

Li, H.B. & Reynolds, J.F. 1993. A new contagion index to quantify spatial patterns of landscapes. *Landscape Ecology* 8: 155–162.

Li, H.B. & Reynolds, J.F. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* 75: 2446–2455.

Lingua, E., Cherubini, P., Motta, R. & Nola, P. 2008. Spatial structure along an altitudinal gradient in the Italian Central Alps reveals competition and facilitation processes among different coniferous species. *Journal of Vegetation Science* 19: 425–436.

Little, R.L., Peterson, D.L. & Conquist, L.L. 1994. Regeneration of subalpine fir (*Abies lasiocarpa*) following fire: effects of climate and other factors. *Canadian Journal of Forest Research* 24: 934–944.

Mac Nally, R. 1996. Hierarchical partitioning as an interpretative tool in multivariate inference. *Australian Journal of Ecology* 21: 224–228.

Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – 'predictive' and 'explanatory' models. *Biodiversity and Conservation* 9: 655–671.

Mac Nally, R. 2002. Multiple regression and inference in ecology and conservation biology: further comments on identifying important predictor variables. *Biodiversity and Conservation* 11: 1397–1401.

McDonald, R.A. 1995. CORONA: success for space reconnaissance, a look into the Cold War, and a revolution for intelligence. *Photogrammetric Engineering and Remote Sensing* 61: 689–720.

Miller, E.A. & Halpern, C.B. 1998. Effects of environment and grazing disturbance on tree establishment in meadows of the central Cascade Range, Oregon, USA. *Journal of Vegetation Science* 9: 265–282.

Moore, I.D., Gessler, P.E., Nielsen, G.A. & Peterson, G.A. 1993. Soil attribute prediction using terrain analysis. *Soil Science Society of America Journal* 57: 443–452.

Moore, I.D., Grayson, R.B. & Ladson, A.R. 1991. Digital terrain modeling: a review of hydrological, geomorphological, and biological applications. *Hydrological Processes* 5: 3–30.

Noble, D.L. & Ronco, F. Jr. 1978. *Seedfall and establishment of Engelmann spruce and subalpine fir in clearcut openings in Colorado*. RM-200. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO, US.

Noble, I.R. 1993. A model of the responses of ecotones to climate change. *Ecological Applications* 3: 396–403.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range: composition and dynamics. *Vegetatio* 45: 3–75.

Resler, L.M. 2006. Geomorphic controls of spatial pattern and process at alpine treeline. *Professional Geographer* 58: 124–138.

Resler, L.M., Butler, D.R. & Malanson, G.P. 2005. Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. *Physical Geography* 26: 112–125.

Rochefort, R.M. & Peterson, D.L. 1996. Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park, Washington, USA. *Arctic, Antarctic and Alpine Research* 28: 52–59.

Rottensteiner, F., Trinder, J., Clode, S. & Kubik, K. 2005. Using the Dempster-Shafer method for the fusion of

LIDAR data and multi-spectral images for building detection. *Information Fusion* 6: 283–300.

Shankman, D. 1984. Tree regeneration following fire as evidence of timberline stability in the Colorado Front Range, USA. *Arctic, Antarctic Alpine Research* 16: 413–417.

Shankman, D. & Daly, C. 1988. Forest regeneration above tree limit depressed by fire in the Colorado Front Range. *Bulletin of the Torrey Botanical Club* 115: 272–279.

Shearer, R.C. 1984. *Effects of prescribed burning and wildfire on regeneration in a larch forest in northwest Montana*. New forests for a changing world: Proceedings of the 1983 convention of the Society of American Foresters. Portland, OR. Washington, DC: Society of American Foresters, pp. 266–270.

Taylor, W.P. 1922. A distributional and ecological study of Mount Rainier, Washington. *Ecology* 3: 214–236.

Terrapoint, L.L.C. 2003. *NASA light detection and ranging (LIDAR) digital elevation products*. The Woodlands, TX, USA.

Tranquillini, W. 1979. *Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European Alps*. Springer, New York, NY, US.

Vale, T.R. 1987. Vegetation change and park purposes in the high elevations of Yosemite National Park, California. *Annals of the Association of American Geographers* 77: 1–18.

Veblen, T.T., Kitzberger, T. & Donnegan, J. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* 10: 1178–1195.

Walther, G.R. 2003. Plants in a warmer world. *Perspectives in Plant Ecology Evolution and Systematics* 6: 169–185.

Wardle, P. 1985. New Zealand timberlines. 3. A synthesis. *New Zealand Journal of Botany* 23: 263–271.

Weisberg, P.J. & Baker, W.L. 1995. Spatial variation in tree regeneration in the forest-tundra ecotone, Rocky Mountain National Park, Colorado. *Canadian Journal of Forest Research* 25: 1326–1339.

Wilson, J.B. & Agnew, A.D.Q. 1992. Positive feedback switches in plant communities. *Advances in Ecological Research* 23: 263–336.

Zar, J.H. 1999. *Biostatistical analysis*. 4th ed. Pearson Education, Delhi, India.

Zevenbergen, L.W. & Thorne, C.R. 1987. Quantitative analysis of land surface topography. *Earth Surface Processes and Landforms* 12: 47–56.

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